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THE
BOTANICAL GAZETTE

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COMPARATIVE ANATOMY OF DUNE PLANTS
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 161

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(WITH THIRTY-FIVE FIGURES)

The literature of ecological anatomy is extensive when one considers that the whole subject of ecology is a late arrival in the field of botany. Comparative anatomy, ecologically viewed, is limited enough to justify a brief review. BONNIER (1) was a pioneer in experimental work, taking parts of plants growing in intermediate situations in the mountains and transplanting one part to the lowlands and another part to alpine conditions. He found that the plants grown in the two habitats differed in appearance, habit, and structure (2). GREVILLIUS (15) in an extensive work on the island Öland compared the vegetation of the alvar, a dry, rocky, treeless plain, with that of the fertile regions. CHRYSLER (7) compared the anatomy of strand plants at Woods Hole with that of the same species growing on the shores of Lake Michigan. CANNON (5) at the Desert Laboratory (Tucson) contributed some experiments on desert plants, keeping some plants under irrigation and letting others of the same species grow without irrigation, his study being a comparison of the conductive tissues. CHERMEZON (6) in a recent contribution to the anatomy of littoral vegetation makes some comparison of it with that of continental plants. All agree that the structure of plants varies with change in conditions.

In 1899 COWLES (8) published the results of his studies of the sand dunes of Lake Michigan, describing the general features of

the coast, the ecological factors, and the plant associations. It was his intention to enter into an investigation of the anatomical relations of the plants described, but other work prevented. In the fall of 1908 he suggested that I undertake the study, and it has been under his direction that the work has been carried on. I wish to express my grateful thanks to him and to all the members of the Department who helped me with criticism and advice, and also to those who aided me in photographic work and in collecting material. In 1904 C. L. HOLTZMAN, in an unpublished dissertation, described the leaves of six of the species included in my work, and I have had access to his paper.

The dune plants were collected from the Indiana dunes, chiefly from the vicinity of Miller's, Dune Park, and Furnessville. The mesophytic forms came mainly from the flood plains of the Desplaines River at Riverside; some were collected in other mesophytic woods in the same general locality, while a few came from the Mississippi flood plain.

The stems and roots were preserved in formalin and 50 per cent alcohol and cut with a hand microtome. The leaves that made the most successful permanent preparations were killed with corrosive sublimate dissolved in 95 per cent alcohol, used hot. These were easily sectioned in paraffin. I found 8μ the most satisfactory thickness. Free-hand sections were also made. Safranin and anilin blue were used in staining. The names are those given in the seventh edition of GRAY's *Manual* and differ therefore at times from those used by COWLES. The drawings were made by the aid of a camera lucida, magnified 470 diameters, and reduced one-half in reproduction.

Ecological factors in the dunes

LIGHT AND HEAT.—There is direct illumination, increased by reflection from the sand. Because of the scanty vegetation and the great exposure, the temperature of the air is higher in summer and lower in winter than in more protected localities. Owing to the high conductivity of sand, the same great divergence between extremes is present in the temperature of the soil.

WIND.—COWLES considers this the most potent factor in determining the character of the dune vegetation. The winds

gather force as they sweep across the lake, and when they reach the shore they gather up sand and carry it along with a force that carves and scars the bark of the trees on the windward side or completely wears it away, as in the case of *Cornus stolonifera*.

SOIL.—The soil is chiefly quartz sand, the particles being relatively large, so that it is extremely porous, which has a great influence on the water and heat relations. As a rule sandy soils are poor in nutrient food materials, nor do they rapidly develop a rich humus because of the rapid oxidation of the organic matter.

WATER.—The surface layer of soil is very dry, as the capillarity of sand is less than that of other soils, evaporation from a sandy surface is rapid, and precipitated water percolates quickly, the water capacity of sand being slight. On the other hand, a sandy soil yields its water to plants more freely than other soils, and below the superficial layer of dry sand there is always a surprising amount of water. FULLER (13) has found this to be more than double the wilting coefficient of dune soil.

BIOTIC FACTORS.—The only biotic factors of marked influence in the dunes are those associated with the plants themselves when they are once established, humus and shade. Humus influences the temperature of the soil and increases the water content, the number of soil organisms, toxicity, and aeration. Shade influences the germination of seeds and increases the accumulation of humus and atmospheric humidity, and so decreases evaporation. FULLER (12) finds that in the cottonwood dunes the evaporation is 21 cc. per day, while on the pine dunes it is 11 cc., in the oak dunes 10 cc., and in the beech-maple forest 8 cc., a descending scale from the pioneer formation to the climax forest.

Description of the plants

I. XEROPHYTIC FORMS

Herbs

Cakile edentula.—A small, very succulent annual. Leaves smooth and thick; outer walls of epidermis 4 μ ; several rows of palisade on each side with a narrow zone of sponge in the center; water-storage tissue about the bundles; stomata on both surfaces; conductive elements not well developed. Stem with epidermal walls thickened all around, the outer 10 μ .

Euphorbia polygonifolia.—A little prostrate succulent annual with abundant latex. Leaves small, thick, inclined to be folded at right angles on the midrib; walls of epidermis thickened, outer 9–12 μ on the upper surface and 15 μ at the edges of the leaf; stomata sunken to the depth of the epidermis; a layer of palisade cells next the upper epidermis and “festoon” palisade about the bundles; a layer of water-storage tissue next the lower epidermis; cells at the bend of the midrib collenchymatous; small development of vascular elements. Stem woody for so small a plant, having a compact vascular cylinder; walls of epidermis thick, outer 8 μ , cuticle 4.6 μ ; cells below thickened; latex tubes conspicuous.

Corispermum hyssopifolium.—Low, branching, succulent annual. Leaf thick, narrow, linear; two layers of palisade on both sides and water-storage tissue in the center; walls of the epidermis thickened, outer 16 μ ; cells with thickened walls about the midrib at the edges of the leaf. Stem with two layers of palisade in the cortex and collenchyma at the surface; walls of epidermis heavy, outer 9.6 μ . Root sclerenchymatous except a few outer layers.

Artemisia caudata and *A. canadensis*.—Stout, bushy biennials or perennials. Leaf divided, divisions thick, smallest almost cylindrical, generally pubescent; double row of palisade on both surfaces, water-storage tissue inside; walls of epidermis thickened, outer wall 6–11 μ ; stomata sunken one-half the depth of the epidermal cells. Stem with pith rapidly reduced after the first year, small in older, a dense cylinder of wood extending almost to the center; great masses of fibers capping the phloem; outer layers of cortex collenchymatous; considerable cork.

Cirsium Pitcheri.—Biennial, tomentose. Leaf very thick, with revolute margins; epidermal cells small, with thickened walls, outer 6.4 μ ; chlorophyll confined to 2–4 outer layers of cells; the rest water-storage tissue with cells increasing in size toward the center with large air spaces between. Stem generally hollow, cortex thick, bundles few, with large vessels and masses of heavy fibers; rays wider than the bundles, the cells with thickened walls, outer cells of cortex collenchymatous.

Lathyrus maritimus.—A smooth trailing perennial herb. Leaf with palisade occupying almost half of the mesophyll, the sponge tissue rather compact; fibers above and below the bundles. Stem sharply angled; phloem capped by a heavy crescent of sclerenchyma; a second ring of sclerenchyma penetrating a distance between the bundles; medullary rays thin; outer wall of epidermis $6.2\ \mu$. Root with large vessels; about one-half the pith made up of scattered masses of sclerenchyma.

Ammophila arenaria.—A stout perennial grass with firm creeping rootstocks that anchor the dunes. Leaf with morphologically upper surface rolled in; the surface a series of ridges and grooves; bundles under the ridges; edges of the leaf and ridges strengthened with hypodermal sclerenchyma, that in the ridges extending into the bundles; upper epidermal cells large and globular, or prolonged into conical hairs; stomata on the upper surface sunken to the depth of the epidermal cells; chlorenchyma reduced to strands each side the bundles; air spaces very small; outer wall of the lower epidermis (the exposed side) $6.4\ \mu$ thick, the cuticle $3.2\ \mu$. Stem with cortical tissue sclerenchymatous; walls of the epidermis slightly thickened all around.

Andropogon scoparius (bunch-grass).—Leaf stiffened with a series of bundles, large ones alternating with three small ones, the space above the small ones filled in with three or four enormous epidermal cells and smaller, hypodermal, colorless cells; epidermal cells occasionally prolonged into sharp hairs, longer than those of *Ammophila*; the large cells collapse at the bend of the leaf, as it folds with the upper surface in; masses of sclerenchyma above and below the large bundles and below the middle of the small ones; chlorenchyma above the bundles; outer wall $9.3\ \mu$; cuticle, thick; stomata on lower surface not sunken.

Calamovilfa longifolia.—A rigid perennial grass with horizontal rootstocks and pubescent sheaths; another dune former. Leaf with lower surface plane; with ridges and narrow depressions on the upper surface which rolls in as in *Ammophila*; walls of epidermis thick, cuticle thick; bundles in the ridges with sclerenchyma above and below, and sometimes about the phloem; hypodermal sclerenchyma next to the lower surface and at the top of the ridges; short,

pointed hairs on the upper surface; chlorenchyma, a layer of palisade, and a layer of spherical cells about the bundles; walls of parenchyma cells sometimes folded in as in *Pinus*; stomata sunken as in *Ammophila*. Stem with bundles more numerous toward the periphery, where the cells of the fundamental tissue become smaller; epidermal cells very small.

Solidago racemosa Gillmani (fig. 1).—A perennial herb, woody at the base. Leaf with outer wall of lower epidermis $8\ \mu$ thick,

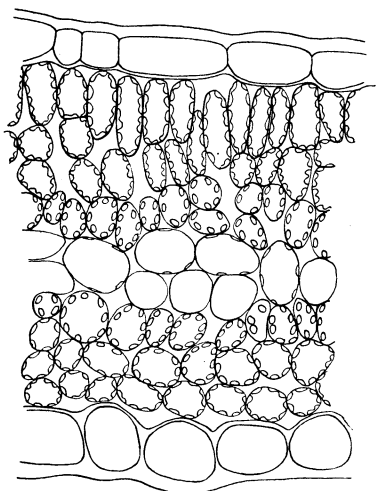


FIG. 1.—*Solidago racemosa Gillmani*: section of leaf.

cuticle $2.4\ \mu$; chlorenchyma above and below; water-storage tissue in the center; chlorenchyma above scarcely palisade-like, but of two or more layers of slightly elongated cells forming a compact tissue; good development of bundles in the midrib. Stem with small pith; cortex thick, containing groups of fibers and occasionally sclereids, outer layers collenchymatous; crystals in the cells of the pith. Root with ground tissue of sclerenchyma; outer cells of cortex collenchymatous.

Lithospermum Gmelini.—A perennial herb clothed with bristly hairs. Leaf thick, coarse, rough on both surfaces, with appressed hairs, bent upward at the midrib; outer wall of epidermis thick on both surfaces, $9.3\ \mu$; palisade next both epidermal layers made up of a row of long cells, or of two rows of shorter cells; three layers in the center almost colorless; stomata not sunken. Stem with a small solid cylinder of wood made up chiefly of fibers, the vessels large; outer layers of cortex slightly collenchymatous; outer wall of epidermis $5\ \mu$ thick.

Arenaria stricta.—A low, tufted herb. Leaf smooth, needle-like; epidermal cells enormous, thickened on all sides especially at the edges of the leaf; outer wall $3.2-7\ \mu$; cuticle thick; sclerenchyma below the bundles; whole mesophyll composed of compact tissue; no palisade; crystals frequent.

Opuntia Rafinesqui.—Stem doing the chlorophyll work; outer wall of epidermis $8\ \mu$ thick, cuticle $2.4\ \mu$; several hypodermal layers of small heavy-walled cells; the chlorenchyma composed of many layers of cells elongated perpendicularly to the surface; the center of the stem occupied by a loose tissue of large colorless cells, the whole retaining water so effectually that it is difficult to dry it out even with heat and pressure; vascular system poorly developed; walls of the elements thin.

Shrubs

Prunus pumila.—A low shrub spreading easily in all directions and thus important in helping to make dunes stationary. Leaf thick, $216\ \mu$; outer wall of epidermis $5\text{--}6\ \mu$; cuticle very thick, ridged on the lower surface, the ridges so high that they fray out along the edge; cells above and below the midrib papillate and cuticle smooth, $8\ \mu$; heavy masses of collenchyma above the stele of the midrib and several layers below, also in other large veins; great development of conductive elements; palisade double and festoon palisade above the bundles in the veins; lower cells of mesophyll palisade-like; crystals, oil, and other deposits abundant. Stem with vessels large and generally numerous; wood fibers heavy, with small lumen; groups of sclerenchyma in the cortex; cork thick.

Salix syrticola.—A shrub with the same habits as *Prunus pumila*. Leaf with upper surface silky, lower hairy, closely serrate, glandular; stipules large; outer wall of upper epidermis thick; heavy sclerenchyma above and below the stele of the midrib, and collenchyma next the epidermis on both sides; two layers of palisade next the upper epidermis and three more layers elongated vertically. Stem with medullary rays very narrow; vessels not large but numerous; fibers heavy, with small lumen; outer layer of pith sclerenchymatous; outer layers of cortex collenchymatous; three rows of mechanical fibers in the cortex, the outermost very wide.

Hudsonia tomentosa.—A bushy, heathlike shrub. Leaf small, awl-shaped, hairy on both surfaces and especially along the edges; upper epidermis composed of large cells; palisade about one-half the mesophyll of the narrow part of the leaf. Stem hairy, very woody, the vascular cylinder occupying most of the diameter, composed of very heavy fibers and few vessels; a few large scleren-

chymatous cells form the pith; a few rows of cells, part of them fibrous, form the cortex.

Arctostaphylos Uva-ursi.—A woody little plant trailing over the ground. Leaf thick, smooth, evergreen; outer wall of epidermis of both surfaces thick, cutinized; side walls plane, cutin sometimes $16\ \mu$ thick; upper epidermis sometimes divided periclinally; bundles compactly developed, with fibers above and below; collenchyma next the epidermis; palisade several rows of shorter cells or two rows of longer; all mesophyll cells elongated perpendicularly to the surface; stomata sunken one-half the depth of the epidermal cells. Stem with xylem cylinder very woody; walls of pith and medullary ray cells heavy; cortex and phloem zones very narrow; cork layer not strikingly thick but very dense; 9 years' growth in a stem 4 mm. in diameter.

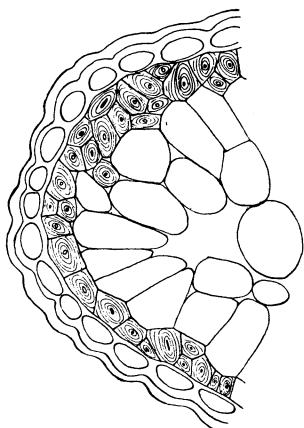


FIG. 2.—*Juniperus communis*: section of leaf.

Juniperus communis (fig. 2).—An erect evergreen shrub. Leaf thick, rigid, convex on one side, concave on the other which is the morphological upper side and is most protected when the leaves are appressed to the stem; stomata on this side at the base of the epidermal cells, guard cells with thickened walls; outer and side walls of epidermis thick, outer $11-13\ \mu$ with cuticle $3.2\ \mu$; hypodermis heavy; resin duct on convex side. Stem with almost no pith and heavy wood cylinder; 13 years' stem 4 mm. in diameter; cork thick.

Juniperus virginiana.—A shrub or small tree. Leaf awl-shaped; outer wall of epidermis very heavy, $9.6\ \mu$, cuticle $4.8\ \mu$; two or three hypodermal layers on the convex side of the leaf heavily thickened; sunken stomata on upper plane surface, the protected side when the leaf is appressed. Stem with solid mass of heavy-walled tracheids and almost no pith; 11 growth rings in a stem 4.5 mm. in diameter; rows of sclereids in the cortex; cork thick.

Hypericum Kalmianum (fig. 3).—A bushy shrub. Leaf revolute, thick, leathery; outer wall of epidermis $4.8\ \mu$, cuticle $2.4\ \mu$, lower epidermal cells inclined to be papillate; double palisade; stomata sunken the depth of the epidermis. Stem with vessels large, fibers heavy, lumen small; pith small, cork thick; three growth rings in a stem 3 mm. in diameter.

Trees

Pinus Banksiana.—Leaf shorter and thicker than in most pines; walls of epidermis heavy; outer $8\ \mu$, cuticle $1.8\ \mu$; hypodermis also heavy; thickness of both increased at the edges of the leaf; outer wall of endodermis thickened and lignified; mesophyll cells with infoldings in the walls; stomata deeply sunken, with an outer and inner vestibule and with walls $3.2\ \mu$ thick; two resin ducts. Stem with small pith; woody cylinder large, composed of a solid mass of tracheids with very thick walls.

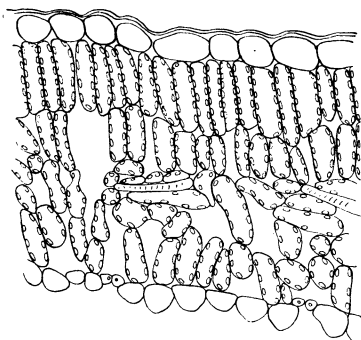


FIG. 3.—*Hypericum Kalmianum*: section of leaf.

Quercus velutina.—Small in comparison with many oaks, and of rather scrubby growth. Leaf thick, having a brilliantly varnished surface; sclerenchyma around the bundles of the midrib; cells above and below collenchymatous; epidermal cells over midrib papillate; outer wall of upper and lower epidermis thickened, cuticle thick; palisade double. Stem with pith star-shaped; vessels large; fibers heavy, with small lumen; medullary rays narrow, pith sclerenchymatous; an irregular band of fibers in the cortex.

Summary of xerophytic characters

The true dune plants have the following characteristics, which, with the exception of the characters of the conductive system, are generally admitted to be xerophytic:

HABIT.—Low, tufted, or bushy, with short internodes (*Arenaria*, *Artemisia*, *Hudsonia*, *Juniperus communis*, *J. virginiana*); low

and spreading (*Prunus pumila*, *Salix syrticola*); low and trailing (*Lathyrus*, *Arctostaphylos*); low, with underground, creeping rootstocks (*Ammophila*, *Calamovilfa*).

LEAF.—Small and awl-shaped (*Arenaria*, *Hudsonia*, *Juniperus communis*, *J. virginiana*); longer, sometimes wide but thick (*Artemisia*, *Ammophila*, *Calamovilfa*, *Lithospermum*, *Prunus*, *Arctostaphylos*, *Pinus*, *Hypericum*, *Cakile*, *Quercus*, *Corispermum*); evergreen (*Arctostaphylos*, *Juniperus communis*, *J. virginiana*, *Pinus*); folded or revolute (*Cirsium*, *Ammophila*, *Calamovilfa*, *Lithospermum*, *Hypericum*, *Euphorbia polygonifolia*); succulent (*Cakile*, *Euphorbia polygonifolia*, *Corispermum*, slight in *Artemisia*, *Cirsium*, *Solidago*); hairy (*Artemisia*, *Cirsium*, *Lithospermum*, *Salix syrticola*, *Hudsonia*); equilateral (*Cakile*, *Corispermum*, *Artemisia*, *Cirsium*, *Lithospermum*).

ANATOMY OF LEAF.—Outer wall of epidermis thick (*Cakile*, *Euphorbia polygonifolia*, *Corispermum*, *Artemisia*, *Cirsium*, *Ammophila*, *Calamovilfa*, *Andropogon*, *Solidago*, *Lithospermum*, *Arenaria*, *Prunus pumila*, *Salix syrticola*, *Arctostaphylos*, *Juniperus communis*, *J. virginiana*, *Pinus Banksiana*, *Hypericum*, *Quercus velutina*, *Opuntia*); cuticle thick (*Ammophila*, *Calamovilfa*, *Andropogon*, *Solidago*, *Arenaria*, *Prunus pumila*, *Arctostaphylos*, *Juniperus communis*, *J. virginiana*, *Pinus Banksiana*, *Hypericum*, *Quercus*, *Opuntia*); deep, compact palisade accompanied by few air spaces in sponge (*Artemisia*, *Lathyrus*, *Lithospermum*, *Prunus pumila*, *Salix syrticola*, *Hudsonia*, *Arctostaphylos*, *Hypericum*, *Quercus velutina*, *Cakile*, *Corispermum*); stomata sunken (*Artemisia*, *Ammophila*, *Calamovilfa*, *Hypericum*, *Euphorbia polygonifolia*, *Arctostaphylos*, *Juniperus communis*, *J. virginiana*, *Pinus*); conductive tissue well developed (*Solidago*, *Prunus*, *Arctostaphylos*); mechanical tissue present as sclerenchyma (*Lathyrus*, *Ammophila*, *Calamovilfa*, *Andropogon*, *Salix syrticola*, *Arctostaphylos*, *Quercus*), as collenchyma (*Solidago*, *Andropogon*, *Prunus*, *Salix syrticola*, *Arctostaphylos*, *Quercus*, *Euphorbia polygonifolia*).

ANATOMY OF STEM.—Succulent (*Opuntia*); conductive tissue well developed, with vessels large (*Cirsium*, *Lithospermum*, *Prunus*, *Hypericum*, *Quercus*), with vessels numerous (*Salix syrticola*, *Prunus pumila*); mechanical tissue present, an abundance of wood

fibers giving general "woodiness" (*Euphorbia polygonifolia*, *Artemisia*, *Cirsium*, *Lithospermum*, *Prunus*, *Salix syrticola*, *Hudsonia*, *Arctostaphylos*, *Pinus*, *Hypericum*, *Juniperus communis*, *J. virginiana*, *Quercus*), as sclerenchyma (*Artemisia*, *Lathyrus*, *Am-mophila*, *Solidago*, *Prunus pumila*, *Salix syrticola*, *Hudsonia*, *Quercus*, *Juniperus virginiana*), as collenchyma (*Artemisia*, *Cirsium*, *Solidago*, *Lithospermum*, *Salix syrticola*, *Pinus*, *Corispermum*); outer wall of epidermis thick (*Cakile*, *Euphorbia*, *Lathyrus*, *Am-mophila*, *Lithospermum*); cork thick (*Artemisia*, *Prunus*, *Hypericum*, *Juniperus communis*, *J. virginiana*).

ANATOMY OF ROOT.—Sclerenchymatous generally (*Cakile*, *Corispermum*, *Lathyrus*, *Solidago*); collenchyma in cortex (*Solidago*); crystals abundant (*Solidago*, *Arenaria*, *Prunus*); resin (*Juniperus communis*, *J. virginiana*, *Pinus*); latex (*Euphorbia*); perhaps none but the last is related to xerophytic conditions.

Slowness of growth is shown by the large number of growth rings in stems of small size (*Arctostaphylos*, *Hypericum*, *Juniperus communis*, *J. virginiana*), testifying to adverse conditions. Succulency usually excludes some other factors, as hairiness and good development of conductive elements.

FITTING (II) has recently shown that desert plants apparently do not need longer roots to reach an abundant water supply, as they have a most effective means of obtaining it from a very scanty supply in the high osmotic pressure of their cell sap. Dune plants have not been examined in this respect. It may be found that they too have this "adaptation" to xerophytic conditions.

II. COMPARISON OF PLANTS GROWING ON THE DUNES WITH THE SAME SPECIES GROWING IN MESOPHYTIC SITUATIONS

The purpose of this part of the investigation was to find out by careful measurements just how much variation there is in species found in two widely differing habitats. The measurements of sections were made with a micrometer divided into 100 spaces. For the measurement of the leaf, sections were made near the middle, cutting straight across the midrib; an average was taken of several measurements of one leaf and then of several leaves. For

the study of the conducting and mechanical tissues of the leaf, a section of the midrib was taken at the base of the blade. For the study of the stems, sections 5 mm. in diameter were used; when this was not possible, the two compared were as nearly equal as obtainable. CANNON'S method of counting was adopted. A circle 14 cm. in diameter was drawn on paper and octants were marked off. With a camera lucida an image of the section was so thrown on the paper that the arc of the octant coincided as nearly as possible with the periphery of the wood cylinder. The area of the octant was 18.24 sq. cm. ($14^2 \times 0.7845 \div 8$). Since the magnification used was 100, the area examined was 0.19 sq. cm. or 19 sq. mm. For the size of the vessels and fibers measurements were always made in the last spring wood, or if that was not fully organized, in the preceding. In the following tables *M* stands for the mesophytic form and *X* for the dune form; *T* for the average thickness of leaf, with minimum and maximum in parenthesis; *UE* for thickness of the upper epidermis, including cuticle; *P* for depth of palisade; *Sp* for depth of sponge; *LE* for thickness of lower epidermis; *OW* for outer wall of the epidermis (including cuticle); and *Cu* for cuticle. The percentages are of the entire thickness of the leaf. In the table of stems *N* stands for the number of vessels in the octant; *D* for the average diameter of the larger vessels, with the maximum in parenthesis; *W*, the thickness of the walls of the vessels; *F*, the thickness of the walls of the fibers; *L*, the lumen of the fibers; *R*, the number of growth rings; *C*, the thickness of cork; and *S*, the thickness of the sclerenchyma ring or of the isolated masses of sclerenchyma that often appear in the cortex. As the size of vessels, being tubes, varies as their cross-sections and as the cross-sections vary as the squares of their radii, it is evident that the vessels in an octant of a mesophytic form would compare with the vessels in an octant of the corresponding dune form as the products of the number of vessels by the squares of their radii. Where the result is not evident at a glance, the radius was squared and the product found. The measurements are all in microns, though the μ is omitted after the first, as is also the per cent sign.

Trees

ACER SACCHARUM

		Leaf		Stem	
	<i>M</i>		<i>X</i>		<i>X</i>
T....	75 μ (69-93)		103 μ (95-109)	N... 41	33
UE...	10.5 = 14 per cent		13 = 12 per cent	D... 36 μ (50)	37 μ (46)
P....	29.5 = 39		40 = 39	W... 3	3.5
Sp...	29.0 = 39		40 = 39	F.... 4.2	4.7
LE...	6.0 = 8		10 = 10	L.... 6.2	8.5
OW...	1.6		3.5	R... 3-5	2-4
Cu...	thin		1.7	C.... 80	72
				S.... 64	50

X.—Hairs on lower surface; upper epidermal cells smaller in depth, slightly larger in surface extent; outer wall and cuticle thicker; sclerenchyma around the bundles of the midrib heavier; greater development of bundles; cuticle on upper surface more strongly ridged. In both stomata on lower surface only.

In all points but the thickness of the walls of the vessels and the fibers, an exception to the majority of cases examined.

CELTIS OCCIDENTALIS

		Leaf		Stem	
	<i>M</i>		<i>X</i>		<i>X</i>
T....	65 μ (87-72)		120 μ (104-144)	N... 17	18.5
UE...	13 = 20 per cent		24 = 20 per cent	D... 74 μ (101)	74 μ (120)
P....	14 = 22		43 = 36	W... 2.4	3.2
Sp...	24 = 37		40 = 33	F.... 4.8	6.4
LE...	14 = 21		13 = 11	L.... 4.8	3.2
OW...	0.7		3	R... 7	7
Cu...	very thin		0.7	C.... 48	32
				S.... 64	80

X.—Large glandular cells frequently occupying the place of the epidermis and palisade; collenchyma below and sclerenchyma above the midrib, where neither appears in the mesophytic form; greater development of vascular elements.—Figs. 4 and 5.

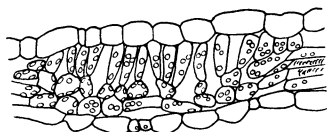
X.—A straggling shrub, probably var. *pumila*; slightly greater development of vessels with heavier walls; fibers heavier, but fewer of them than in *M*, replaced by tracheids; cork thinner; more sclerenchyma in the cortex.

FRAXINUS AMERICANA

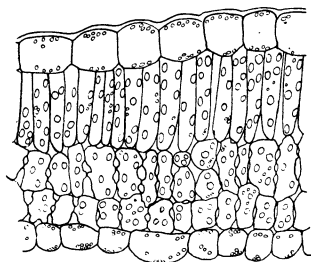
Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 142 μ (124-159)	162 μ (142-187)	N... 22.5	19.5
UE... 11 = 8 per cent	14 = 9 per cent	D... 53 μ (87)	51 μ (72)
P.... 52 = 36	68 = 42	W... 3.7	3.9
Sp.... 68 = 48	59 = 36	F... 3.2	4.5
LE... 11 = 8	21 = 13	L.... 7.2	7.3
OW... 1.5	3	R... 88	110
Cu... 0.7	1.8	C... 53	99
		S.... 3-5	1-2

X.—Epidermal cells of greater depth; outer wall and cuticle thicker, ridged in the lower epidermis, most of the cells of the lower epidermis produced into short conical hairs, the rest into long hairs (*M* smooth); all tissue more compact; palisade deeper, tending to develop four rows (*M* only two); vessels in the midrib more numerous but not larger; walls thicker; greater development of fibers about the stele. Both have conspicuous glands on the upper surface, and stomata on lower surface only.—Figs. 6 and 7.

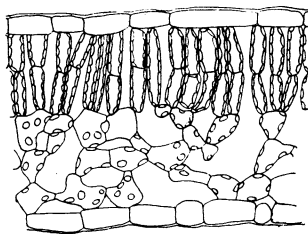
X.—Differing from the majority in number and size of vessels and more rapid growth; walls of vessels and fibers thicker; sclerenchyma and cork heavier. In both walls of pith-cells thickened with conspicuous canals, and outer cortex collenchymatous, features pronounced in *X*.



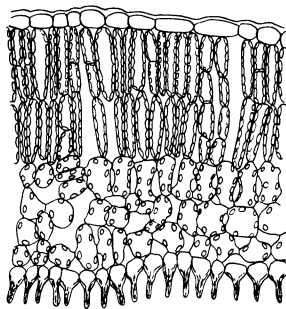
4



5



6



7

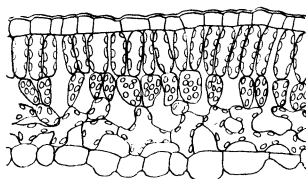
FIGS. 4-7.—Figs. 4 and 5, *Celtis occidentalis*: sections of leaves; fig. 4, mesophytic form; fig. 5, dune form; figs. 6 and 7, *Fraxinus americana*: sections of leaves; fig. 6, mesophytic form; fig. 7, dune form.

JUGLANS CINEREA

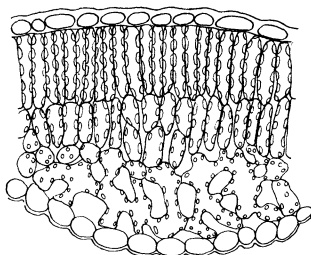
Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 92 μ (79-112)	148 μ (119-166)	N... 18	25
UE... 12 = 13 per cent	13 = 9 per cent	D... 64 μ (85)	55 μ (79)
P.... 21 = 21	39 = 26	W... 7.3	3.8
Sp.... 44 = 48	82 = 55	F.... 4	3.2
LE... 14 = 16	14 = 10	L.... 9.5	9
OW... thin	3.7	R... 1-6 (av. 3)	1-3
		C.... 60	.57
		S.... 73	77

X.—More pubescent; upper epidermal cells smaller in depth, same in surface extent; first layer of palisade deeper and a second layer developed; vessels in midrib of the same size but more numerous; more sclerenchyma and collenchyma; crystals abundant.—Figs. 8 and 9.

X.—Like the majority in the greater number of vessels of smaller area (but the final product greater), the smaller lumen of the fibers, and the heavier sclerenchyma; differing in thinner walls and cork, and occasionally large number of rings produced in *M*



8



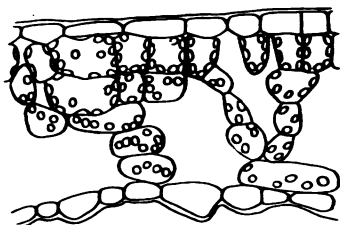
9

FIGS. 8, 9.—*Juglans cinerea*: sections of leaves; fig. 8, mesophytic form; fig. 9, dune form.

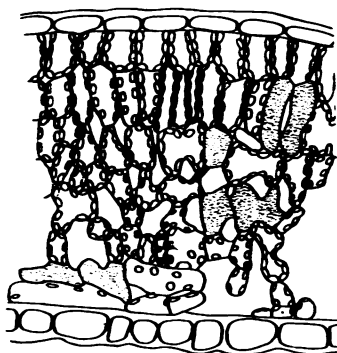
LIRIODENDRON			
Leaf		Stem	
M	X	M	X
T.... 148 μ (137-168)	210 μ (190-236)	N... 79	131
UE... 15 = 10 per cent	17 = 8 per cent	D... 34 μ (48)	32 μ (41)
P.... 37 = 25	59 = 28	W... 3.1	3.2
Sp.... 80 = 54	111 = 53	F.... 3.8	4.6
LE... 16 = 11	22 = 11	L.... 10.7	8.5
OW... 3.3	5.6	R... 1-3	2-5
Cu	2	C.... 42	50
		S	

X.—Cells of upper epidermis smaller in surface and depth, side walls plane (wavy in M); palisade deeper, sometimes of more layers; cells of upper layer each side of midrib larger than others and without chloroplasts, as if a secondary epidermis; vessels more numerous in midrib; greater masses of fibers and more collenchyma. In both, lower epidermis heavy.—Figs. 10 and 11.

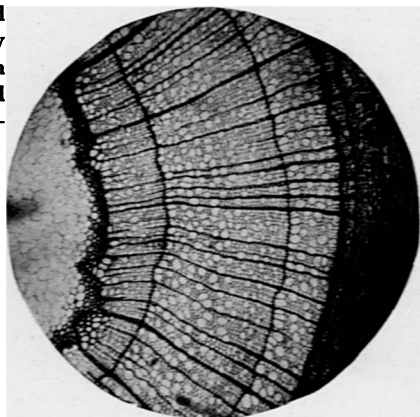
Like the majority in all respects. In both, sclerenchyma around the pith and groups of fibers capping the phloem.—Figs. 12 and 13.



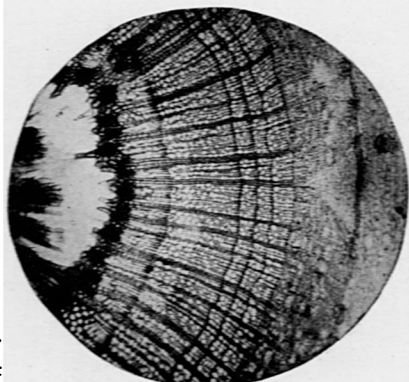
10



11



12



13

FIGS. 10-13.—*Liriodendron tulipifera*: sections of leaves; fig. 10, mesophytic form; fig. 11, dune form; sections of stems; fig. 12, mesophytic form; fig. 13, dune form.

OSTRYA VIRGINIANA

Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 78 μ (66-95)	110 μ (91-125)	N... 24	59
UE... 10 = 11 per cent	11 = 10 per cent	D... 48 μ (75)	26 μ (37)
P.... 30 = 38	43 = 39	W... 2.8	2.5
Sp.... 32	45	F.... 3.3	3.9
LE... 6	11	L.... 6.7	5.6
OW... 1.3	3.2	R... 3	3-6
		C.... 29	64

X.—Upper epidermis slightly thicker and wall thicker; little variation in the depth of the palisade, but the layer more compact; stomata on lower surface only (in *M* occasionally on the upper).

X.—Rings of sclerenchyma in the cortex wider and outer layers of the pith more sclerenchymatous; in all respects, except as to the thickness of the wall of the vessels, agreeing with the majority.

POPULUS BALSAMIFERA

Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 257 μ (243-272)	212 μ (195-228)	N 33	90
UE... 18 = 7 per cent	17 = 8 per cent	D... 46 μ (62)	36 μ (50)
P.... 96 = 37	94 = 44	W... 2.9	2.6
Sp.... 129	89	F.... 4.1	3.8
LE... 14	16	L.... 7.2	6.8
OW... 4.3	5	R... 1-2	2-9
Cu... 1	1.2	C....	100
		S.... 64	90

The only exception found to the general fact that dune plants have thicker leaves than mesophytic. *X*.—Upper epidermis and palisade relatively deeper; outer wall and cuticle thicker and ridged; more vessels in the midrib, larger; more fibers about the stele. Both have stomata on both surfaces; all side walls of epidermis plane except those of lower surface in *M*; double palisade.

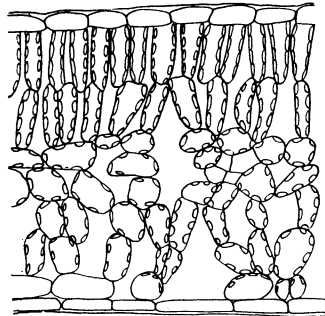
X.—Vessels agreeing with the majority in total area, but walls slightly thinner, walls of fibers also thinner, but lumen smaller, so the amount of wood may be the same; cork only starting to form in *M*.

POPULUS DELTOIDES

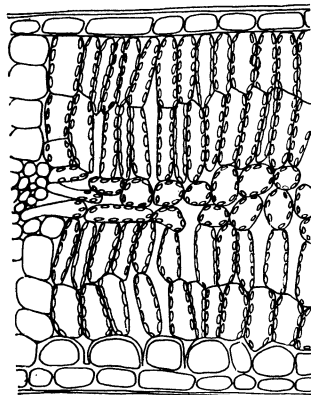
Leaf		Stem	
M	X	M	X
T.... 193 μ (177-227)	254 μ (236-295)	N... 46	85
UE... 13 = 7 per cent	18 = 7 per cent	D... 49 μ (64)	50 μ (62)
P.... 62 = 32	84 = 33	W... 2.6	2.7
Sp.... 105 = 54	138 = 55	F... 3.8	3.9
LE... 13	14 = 5	L.... 6.8	6
OW... 2.3	4	R... 2	1-4
Cu... 0.8	1.3	C... 82	105
		S... 94	98

In both lower epidermis thickened as well as upper, stomata on both surfaces and side walls of epidermal cells plane, all related to the movement of the leaf. X.—Upper epidermal cells smaller in surface; surface slightly hairy; palisade sometimes triple; also palisade cells near lower epidermis, separated from it by a layer of heavily walled cells, like a secondary epidermis. Other points follow the general rule.—Figs. 14 and 15.

Agreeing with the majority in all points; a tendency to angled twigs and star-shaped pith more marked in X.



14



15

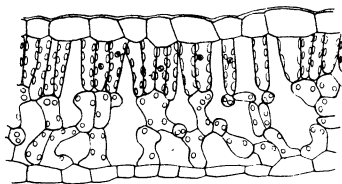
FIGS. 14, 15.—*Populus deltoides*: sections of leaves; fig. 14, mesophytic form; fig. 15, dune form.

TILIA AMERICANA

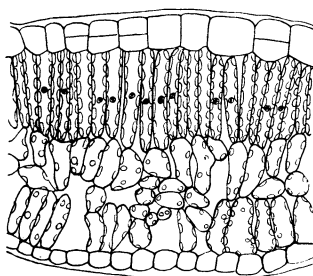
Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 90 μ (90-108)	138 μ (135-156)	N... 59	63
UE... 17 = 19 per cent	23 = 17 per cent	D... 38 μ (53)	41 μ (41)
P.... 26 = 29	45 = 33	W... 2.7	2.8
Sp... 36 = 46	52 = 38	F... 2.8	2.4
LE... 11 = 12	17 = 12	L... 9.6	9.1
OW... 3.7	4.4	R... 2-5	1-5
Cu... 1.5	2	C... 58	50

X.—Cells of upper epidermis smaller in depth, larger in surface, sometimes divided periclinally; side walls on lower surface wavy, upper and both in *M* plane; deeper palisade and tendency toward second layer; midrib as in preceding *X*. In both hairs in the axils of the veins; cuticle ridged.—Figs. 16 and 17.

In both bands of sclerenchyma in the phloem and collenchyma under the cork, slightly less in *X*; little variation in walls and lumina of the fibers, but vessels more numerous and larger in *X*.



16



17

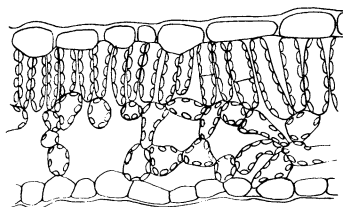
FIGS. 16 and 17.—*Tilia americana*: sections of leaves; fig. 16, mesophytic form; fig. 17, dune form.

ULMUS AMERICANA

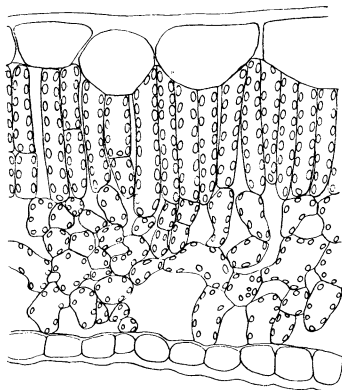
Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 102 μ (94-109)	174 μ (164-186)	N... 28.5	52
UE... 21 = 21 per cent	38 = 22 per cent	D... 61 μ (104)	61 μ (96)
P.... 29 = 29	70 = 40	W... 3.7	3.3
Sp.... 38 = 37	51 = 29	F.... 5.9	5.7
LE... 13 = 13	15 = 9	L.... 2.9	3.7
OW... 3.2	5.2	R... 5-11	5
Cu... thin	thin	C.... 66	66

X.—Cells of upper epidermis greater in depth; side walls plane, cuticle not ridged (in *M* walls slightly wavy and cuticle slightly ridged on lower surface); palisade deeper sometimes double, midrib structure as in other *X*. In both upper surface rough, hairy (*X* more so); some epidermal cells enormous.—Figs. 18 and 19.

Vessels as in majority. *X*.—Walls of vessels and of fibers very slightly thinner than in *M* and lumina of fibers larger, yet masses of fibers so much more numerous they form more wood; cork and cortical sclerenchyma the same.



18



19

FIGS. 18 and 19.—*Ulmus americana*: sections of leaves; fig. 18, mesophytic form; fig. 19, dune form.

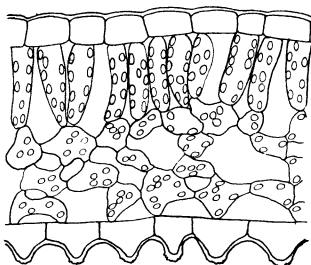
Shrubs

CORNUS STOLONIFERA

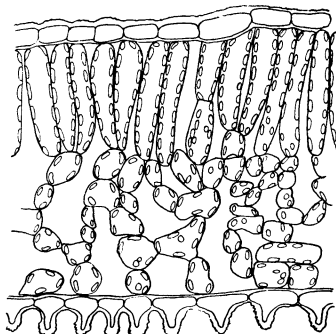
Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 129 μ (120-144)	156 μ	N... 63	70
UE... 17 = 13 per cent	15 = 10 per cent	D... 30 μ (41)	33 μ (45)
P.... 34 = 26	48 = 31	W... 3.2	34
Sp... 56 = 44	72 = 46	F... 4.7	5
LE... 22 = 17	21 = 13	L... 6.4	6.2
OW... 1.6	2	R... 1-3	2-8
Cu... thin	0.8	C... None except at lenticels	112 (in 8-year stem)

X.—Hairs more abundant than in *M*, on upper surface radiating from a center parallel to the surface, tuberculate; on lower surface simple or branched; short hairs also found, formed as slight prolongations of most of the lower epidermal cells, their cuticle prominently ridged; cells of upper epidermis smaller in all dimensions; side walls plane (wavy in *M*); deposits in the form of crystals and oil in the cells, and wax on the outer wall; other points as in most xerophytic forms.—Figs. 20 and 21.

Epidermal cells when present papillate and cuticle heavy; cork not formed before 5 years. In both small groups of sclerenchyma in cortex. All points as in majority.



20



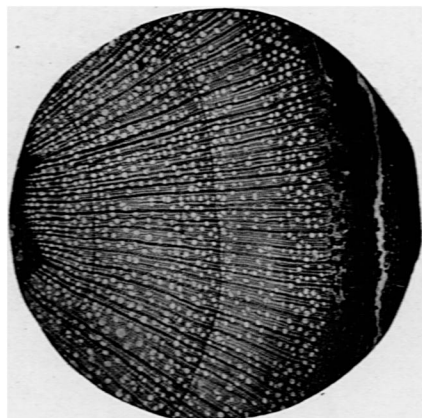
21

FIGS. 20, 21.—*Cornus stolonifera*: sections of leaves; fig. 20, mesophytic form; fig. 21, dune form.

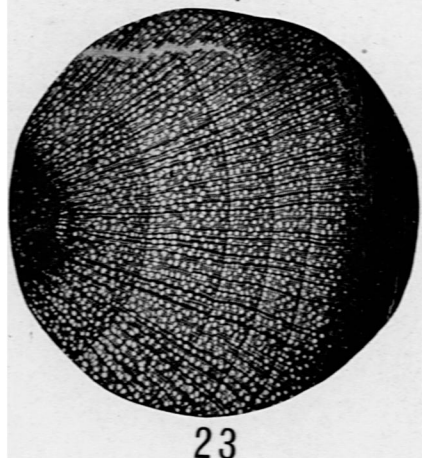
HAMAMELIS VIRGINIANA

Stem (figs. 22 and 23)

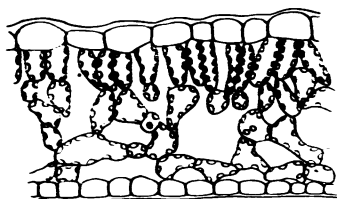
	<i>M</i>	<i>X</i>
N...	94	157
D... 29	μ (37)	24 μ (27)
W...	2.3	1.6
F....	5.7	6.4
L....	5.6	4
R...	3	5
C....	56	48
S....	64	88



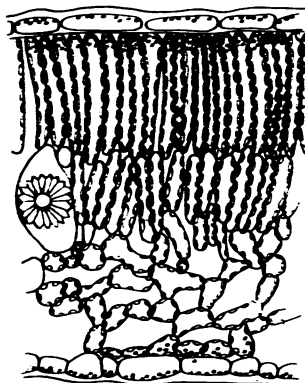
22



23



24



25

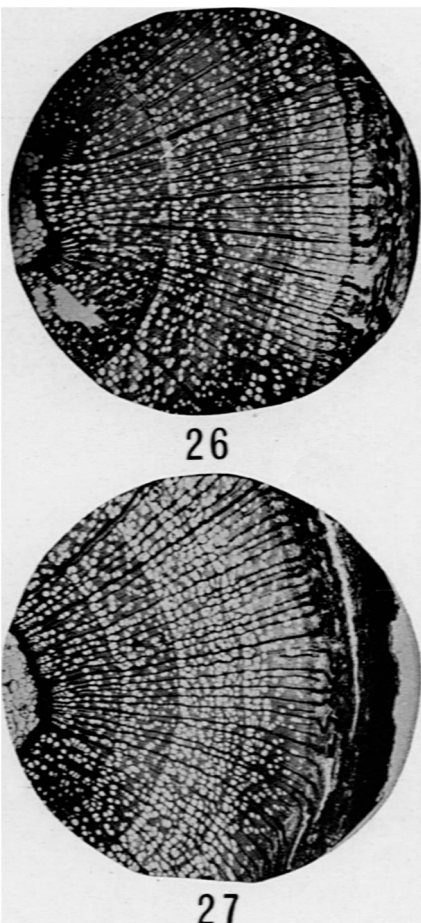
FIGS. 22-25.—Figs. 22 and 23, *Hamamelis virginiana*: sections of stems; fig. 22, mesophytic form; fig. 23, dune form; figs. 24 and 25.—*Prunus virginiana*: sections of leaves; fig. 24, mesophytic form; fig. 25, dune form.

PRUNUS VIRGINIANA

Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 119 μ (100-123)	198 μ (187-214)	N... 76	108
UE... 18 = 15 per cent	16 = 8 per cent	D... 38 μ (55)	35 μ (45)
P.... 35 = 30	99 = 50	W... 3.1	3.5
Sp.... 51 = 43	66 = 33	F.... 4.6	4.6
LE... 14 = 12	17 = 9	L... 4.7	4.4
OW... 2.9	6.7	R... 3	3-6
Cu... 1.1	1.8	C.... 42	61
		S.... 83	51

X.—Hairs on lower surface (none in *M*); cells of upper epidermis larger in surface, of less depth, cuticle more prominently ridged than in *M*; side walls less wavy; palisade double (sometimes so in *M*, but cells are not so long nor so compact as in *X*); midrib as in other *X* (sometimes in *M* sclerenchyma below the stele is scarcely perceptible); oil drops, especially in epidermis and upper part of palisade; crystals and other deposits about the bundles.—Figs. 24 and 25.

Only exception to the majority rule is the sclerenchyma, which is heavier in some mesophytic forms.—Figs. 26 and 27.



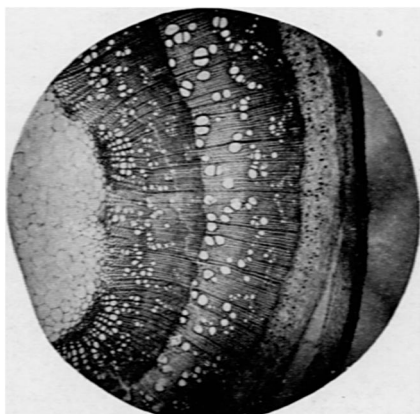
FIGS. 26-27.—*Prunus virginiana*: sections of stems; fig. 26, mesophytic form; fig. 27, dune form.

PTELEA TRIFOLIATA

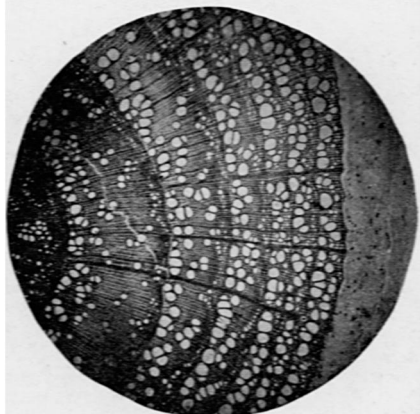
Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T 147 μ (131-156)	185 μ (177-193)	N ... 51	51
UE... 14 = 9 per cent	18 = 10 per cent	D ... 53 μ (73)	55 μ (82)
P 42 = 29	56 = 30	W... 2.2	3.1
Sp ... 78 = 53	95 = 51	F.... 2	2.9
LE... 13 = 9	16 = 9	L.... 8.4	7.2
OW .. 1.2	4.8	R ... 2-3	4-7
Cu ... thin	1.3	C ... 50	83

X.—Hairs abundant on lower surface (none in *M*); cells of upper epidermis slightly larger in surface; side walls on both surfaces plane and cuticle ridged (in *M* wavy and only slightly ridged); palisade, sponge, and midrib as in other *X*. One tree in an especially exposed situation, near the top of a wind sweep leading up from the lake, probably once a mesophytic pocket, had a more pronounced structure than the one figured; the leaf averaged 210 μ in thickness, with an outer wall 6.4-8 μ , heavily cutinized.

Agreeing with the majority, except that collenchyma in outer cortex may be no heavier in *X*.—Figs. 28 and 29.



28



29

FIGS. 28-29.—*Ptelea trifoliata*: sections of stems; fig. 28, mesophytic form; fig. 29, dune form.

SALIX LONGIFOLIA

Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 152 μ (136-168)	188 μ (162-212)	N... 77	66.5
UE... 8 = 5 per cent	12 = 6 per cent	D... 36 μ (53)	43 μ (55.5)
Mes... 133 = 88	165 = 88	W... 2.4	2.4
LE... 11 = 7	11 = 6	F.... 2.8	3
OW... 1.5	3	L.... 5.3	6.7
Cu... thin	2	R... 4	2
		C.... 33	32
		S.... 33	48

Equilateral; two rows of palisade on each side beneath a hypodermis, differentiated as a special storage region; stomata on both surfaces, slightly sunken. *X*.—Upper palisade cells more elongated; sclerenchyma and collenchyma more abundant in midrib.

X.—Agreeing with the majority in the greater area of vessels and greater number and size of sclerenchyma masses in the cortex; exceptional in the larger lumen of the fibers and fewer growth rings.

Lianas

CELASTRUS SCANDENS

Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 101 μ (92-123)	164 μ (138-174)	N... 36	37
UE... 14 = 14 per cent	22 = 14 per cent	D... 54 μ (78)	45.5 μ (69)
P.... 25 = 25	43 = 26	W... 2.8	3.6
Sp... 49 = 48	81 = 49	F.... 4.9	4.5
LE... 13 = 13	18 = 11	L.... 8.4	7.5
OW } thin	4	R... 1-3	1-3
Cu } thin	1.7	C.... 80	76

X.—Coarse, often merely acute; veins prominent on the under side. *M*.—Smooth and fine, long acuminate; veins not prominent on under side; other variations as usual.

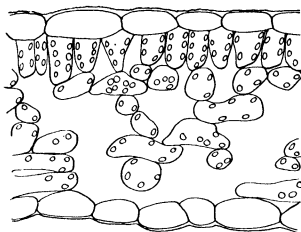
Chiefly an exception; *M* greater in area of vessels, heavier fibers and cork. *X* follows the majority in having heavier sclerenchyma around the pith, thicker walls of the vessels, and smaller lumina in the fibers.

PSEDERA QUINQUEFOLIA

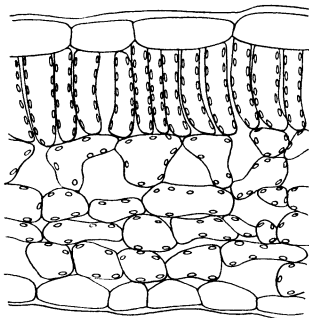
Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 110 μ (99-130)	183 μ (164-195)	N... 36	40.5
UE... 14 = 13 per cent	21 = 11 per cent	D... 78 μ (120)	61 μ (90)
P.... 24 = 22	56 = 31	W... 2.8	3.4
Sp... 59 = 53	90 = 49	F.... 4.6	5.9
LE... 13 = 12	16 = 9	L.... 7.2	4.7
OW... 1.5	3	R... 1	1.2
Cu... 0.7	1.5	C.... 196	188
		S... 112	62

In both side walls of epidermal cells plane except in lower surface of *M*, cuticle ridged, hairs on the lower surface. *X*.—Epidermal cells larger in surface, smaller in depth; other points as usual except there is not greater development of conductive tissues.—Figs. 30 and 31.

Exceptional in the smaller area of cross-sections of vessels in *X*, less sclerenchyma and cork; the cork is loose and shreds off, so more may have been lost in *X* than in *M*; the other points agree with the majority.



30



31

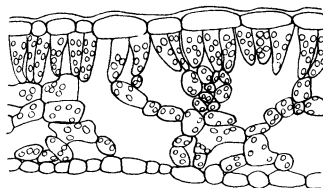
FIGS. 30, 31.—*Psedera quinquefolia*: sections of leaves; fig. 30, mesophytic form; fig. 31, dune form.

RHUS TOXICODENDRON

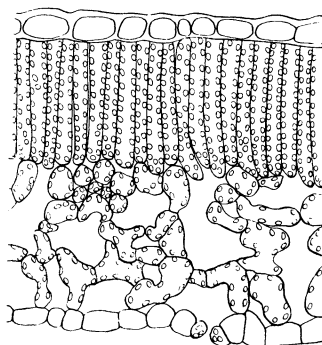
Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 79 μ (73-116)	140 μ (123-198)	N... 35.5	18.5
UE... 9 = 11 per cent	12 = 9 per cent	D... 85 μ (99)	69 μ (88)
P.... 25 = 33	45 = 32	W... 2	2.4
Sp... 37 = 46	70 = 56	F... 2.4	2.8
LE... 8 = 10	12 = 9	L... 9.6	7.2
OW... 1.9	2.7	R... 2	3
Cu... thin	1.4	C... 183	145

X.—Epidermal cells smaller in depth; occasional indications of a double palisade; other points as usual.—Figs. 32 and 33.

Exceptional but in the mass of wood formed.



32



33

FIGS. 32-33.—*Rhus toxicodendron*: sections of leaves; fig. 32, mesophytic form; fig. 33, dune form.

SMILAX HISPIDA

Leaf		Stem	
		(Quadrant used instead of octant)	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 106 μ (96-129)	168 μ (157-204)	N... 6 bundles; each	6
UE... 11 = 11 per cent	22 = 13 per cent	with 2 large	2
Mes... 82 = 77	124 = 74	vessels and 18	13
LE... 13 = 12	22 = 13	smaller	
OW... 1.5	3.7	D... of large ves-	
Cu... thin	1	sels 105	107
		W... 4	4
		F... 3.2	3.6
		L... 5.9	4.3
		OW.. 18	22

X.—Epidermal cells deeper and larger in surface extent; outer wall and cuticle heavier; cuticle more strongly ridged; side walls less wavy; more conductive and mechanical tissues, but walls thinner. The mesophyll shows the usual monocot variation, no differentiation into palisade and sponge.

X.—Two vessels larger, but not so many small ones; cortex more collenchymatous; pith cells with thicker walls, pith packed with starch grains and crystals.

VITIS VULPINA

Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 105 μ (100-118)	153 μ (127-164)	N... 9	10
UE... 14 = 13 per cent	13 = 9 per cent	D... 105 μ (142)	102 μ (127)
P.... 28	45 = 29	W... 4	4.5
S.... 50	81 = 53	F... 5.2	4.8
LE... 13	14 = 9+	L... 7.2	7.1
OW {	1.8	R... 2-3	2-3
Cu } thin	1	C... 236	307

X.—Upper epidermal cells smaller in depth, larger in surface; hairs on veins on both surfaces (only on upper in *M*); other points as usual. In both walls plane and cuticle somewhat ridged.

X.—Slightly more area in cross-sections of vessels; cork thicker; less sclerenchyma.

Herbs

ASCLEPIAS SYRIACA

Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 225 μ (230-296)	272 μ (237-304)	N..... 25	18
UE... 25 = 10 per cent	25 = 9 per cent	D..... 46 μ (66)	64 μ (87)
P.... 54 = 21	77 = 28	W..... 3.5	4.6
Sp.... 158 = 62	151 = 56	F..... 2.9	3.5
LE... 18 = 7	19 = 7	L..... 17	15
OW... 2.4	2.4	OW..... 4	6.4
		Wood cyl 185	611

In both side walls of upper epidermal cells plane, of lower wavy; cuticle ridged on lower surface. *X*.—Hairs on both surfaces (only on lower in *M*); upper epidermal cells smaller in depth, larger in surface; palisades often deep in proportion to sponge; where not, a secondary palisade partly organized; conductive and supporting tissues as usual; latex and other secretions more abundant.—Figs. 34 and 35.

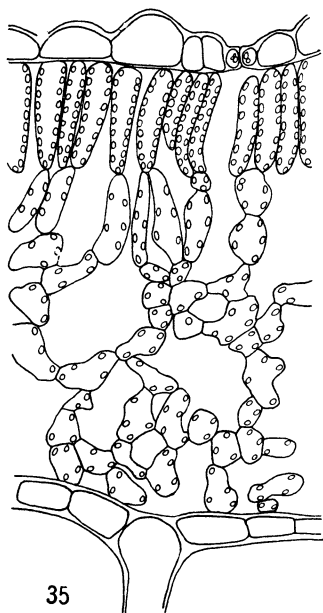
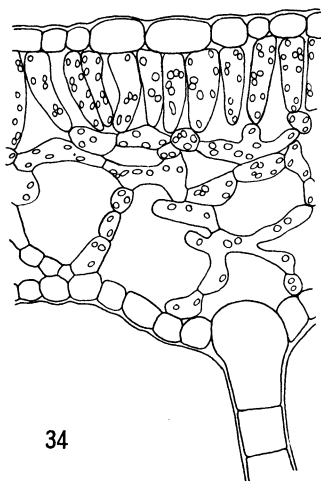
X.—Area of cross-sections of vessels smaller, larger cylinder of wood formed; walls of vessels and of fibers heavier, lumen of fibers smaller, so more wood; outer wall of epidermis and hypodermal collenchyma heavier.

SMILACINA STELLATA

Leaf		Stem	
<i>M</i>	<i>X</i>	<i>M</i>	<i>X</i>
T.... 174 μ (155-199)	202 μ (182-242)	Bundles in field... 12	12
UE... 28 = 16 per cent	30 = 15 per cent	N in bundle..... 15	13
M.... 119 = 68	144 = 71	D..... 27 μ	32 μ
LE... 27 = 16	29 = 14	W..... 4.3	4.5
OW... 2.6	2.9	OW..... 7.2	6.4
Cu... 0.7	0.7		

X.—Epidermal cells smaller in depth, larger in surface; hairs more abundant, more crystals deposited; other variations as usual; in both no differentiation in the mesophyll, the general monocot situation; side walls of epidermal cells plane.

X.—Area of cross-sections of vessels greater; walls of vessels heavier, but outer wall thinner.



FIGS. 34, 35.—*Asclepias syriaca*: sections of leaves; fig. 34, mesophytic form; fig. 35, dune form.

Swamp forms

Sometimes a moving dune passes over a swamp association, and the members by increased length of stem keep pace with it for a time; a few of these have been examined and compared with forms growing in their natural habitat.

PLATANUS OCCIDENTALIS					
Leaf			Stem		
S		X	S		X
T.... 152 μ (136-162)		199 μ (162-205)	N.... 66		69
UE... 23 = 15 per cent		25 = 12 per cent	D.... 35 μ (50)		46 μ (63)
P.... 52 = 34		63 = 32	W.... 3.2		3.2
Sp.... 62 = 41		92 = 46	F.... 5		3.2
LE... 16 = 10		19 = 10	L.... 6.4		7
OW... 4		2.8	R.... 3		2
			C.... 68		6.9
			S.... 100		116
			Collen 56		109

The dune form has thicker leaves than the swamp form, but the palisade and outer wall of the epidermis are exceptional.

The dune form shows an increase in number and size of the vessels, but there is no increase in woody tissue furnished by the fibers. There seems to be no diminution in growth as indicated by the growth rings, but mechanical tissue outside the stele and the cork have increased.

ALNUS INCANA			
Stem			
S		X	
N.....	68	61	Swamp form, vessels larger than the others but fewer in number. Dune form, larger area of vessels. Thickness of walls about the same.
D.....	29	34	
W.....	2.5	2.6	
F.....	3.5	3.4	
L.....	7	8.8	

CEPHALANTHUS OCCIDENTALIS			
Leaf			
S		X	
T... 175 μ (143-168)		163 μ (147-189)	A second layer of palisade is partly organized in the swamp form and completely in the dune form. The first palisade is relatively shorter in the dune form, but the second is so much more compact than in the swamp form that it must more than make up the amount of tissue. In both forms stomata are found on the lower surface only and the side walls of the epidermal cells are waxy.
UE 16 = 9 per cent		17 = 10 per cent	
P... 54 = 31		48 = 29	
Sp.. 91 = 52		84 = 52	
LE. 14 = 8		14 = 9	
OW 3		3.7	
Cu. 1.6		2	

SALIX GLAUCOPHYLLA

Leaf		Stem	
M	X	S	X
T.... 185 μ (180-208)	231 μ (219-240)	N.... 57	64
UE... 20 = 10 per cent	19 = 9 per cent	D.... 45	47
P.... 92 = 50	120 = 52	W.... 2.3	2.4
Sp.... 57 = 31	69 = 30	F.... 3.1	4.8
LE... 16 = 8	19 = 9	L.... 5	3.2
OW... 4.3	4.8	R.... 2-4	4
Cu... 1.6	1.6	Cork.. 56	80
		Collen 4-6 layers	7 layers

Little variation, but the palisade is slightly deeper in the dune form; the vessels of the midrib are larger though about as numerous, their walls are heavier as is also the outer epidermal wall, and there is more collenchyma.

In the dune form more vessels and larger; the fibers heavier and the lumina smaller, giving more wood; growth rings about the same; more cork, collenchyma, and sclerenchyma.

CORNUS STOLONIFERA

A plant growing on the edge of a river was partly submerged by a dune. The stem was examined to find the difference between the submerged and the aerial parts.

	Submerged	Aerial
Cortex and phloem.....	400 μ	380 μ
Wood cylinder.....	836	950
Pith.....	1976	1482
	<hr/> 3212	<hr/> 2812

The upper exposed part is not as large as the submerged part, but the wood cylinder is larger.

	Submerged	Aerial
N.....	62	44
D.....	23	38
W.....	2.3	3.2
F.....	5.1	5.6
L.....	10.4	5.6

In a given area in the cylinder there are fewer vessels, larger in diameter but less in area, which must be more than compensated for by the size of the whole cylinder. The walls of the vessels and fibers are heavier and the lumina of the fibers smaller, giving more wood.

SALIX LONGIFOLIA

Situation the same, but the parts examined were not parts of the same stem, but were of the same size.

	Submerged	Aerial
N.....	42	51
D.....	41	43
W.....	3.2	2.4
F.....	3	3.2
L.....	7.7	6.8

In aerial stem more and larger vessels, walls slightly thicker, lumina of fibers smaller, giving more wood.

The swamp forms on the whole show the same variations as the mesophytic forms.

Table (I) on p. 298 gives a comparison of mesophytic and dune forms of the same species with respect to eleven characters of the leaf.

A summary of leaf characters is as follows:

Hairs more abundant.....	12 X	(3 same)
Surface of upper epidermal cells greater.....	9 X- 5 M	(2 same)
Depth of upper epidermal cells greater.....	5 X-12 M	(4 same)
Side walls of upper epidermal cells wavy.....	6 X-11 M	
Side walls of lower epidermal cells wavy.....	8 X-16 M	
Outer wall of epidermis heavier.....	18 X	(2 same)
Cuticle ridged.....	10 X- 6 M	
Palisade more completely organized.....	17 X	(1 same)
Better development of conductive elements.....	15 X- 2 M	(1 same)
Heavier sclerenchyma.....	14 X- 1 M	(1 same)
Heavier collenchyma.....	17 X	

All leaves, with the exception of those of *Populus balsamifera*, were thicker in the dune form than in the mesophytic. The poplar was growing alone at the side of a road, so the exposure was greater than in the woods where most of the mesophytic specimens were collected. The bud scales also were thicker, and in most cases the outer wall, or the cork if it had developed, was thicker.

The greater extent of surface in the upper epidermal cells in the majority of the dune forms is striking. GREVILLIUS speaks of epidermal cells in the alvar plants being smaller than in the normal, but he may have used the lower surface only, as he mentions the subject in connection with stomata, and that may differ from the upper surface. Cuticular transpiration is reported as taking place from the side walls of the epidermal cells more abundantly than from the lumen of the cell. If this is true, then increase in the surface extent of the cell would decrease cuticular transpiration. The apparent thickness of the epidermis of dune forms is due to the heavy wall and cuticle and not to the depth of the cells. Waviness of the side walls seems to be related to shade, as it occurs more frequently in mesophytic leaves, and in mesophytic leaves on the under side. Ridging of the cuticle accompanies great thickness. Deep, compact palisade, well developed conductive elements, heavy sclerenchyma, and the presence of hairs are characters noted

in true dune plants and generally admitted to be xerophytic. Stomata appear only on the under sides of leaves of both forms except in the cases noted, where they appear on both sides; there is no variation except in the one tree *Ostrya* which sometimes has stomata on the upper surface also. Occasionally specimens from mesophytic situations in the dunes show interesting variations. In these places a great deal of humus has collected above the sand, changing the water content and other soil relations, and xerophytic pioneers have made enough shade and protection for mesophytic forms to come in, so woods have developed. The exposure must be less here and the water relations better than on dunes with scantier vegetation, yet leaves of *Fraxinus*, *Cornus*, and *Ostrya* collected in these woods were thicker than some of the dune forms. The internal structure of *Fraxinus* differed from the dune form, the palisade consisting of a single layer of cells, not compactly arranged.

Another interesting variation comes out in the comparison of leaves of different seasons. Those collected in 1911 are frequently thicker than those collected in 1909 in the same habitat, so that the mesophytic form of 1911 is sometimes thicker than the xerophytic form of 1909, but the xerophytic form of 1911 is correspondingly increased. The season was an unusual one, showing temperatures of 39°, 46°, and 66°, for March, April, and May, in which time the leaves became fully mature, the normal being 34.4°, 45.9°, and 56.5°. In 1909 the temperature was very near the normal. The normal percentages of possible sunshine are 52, 60, and 64, while 1911 had 63, 54, and 79, so March and May were considerably above the average, though April went below. Precipitation was near the normal except in March, when it was only a little more than half. Winds were not unusually high. The variation in thickness must have been due, at least in part, to the unusually high temperature in the three months, sunshine above the average in March and May, and small precipitation in March.

The accompanying table (II) gives a comparison of mesophytic and dune forms as to nine characters of the stem.

TABLE II
STEM CHARACTERS OF MESOPHYTIC AND DUNE FORMS COMPARED

	Acer	Asclepias	Celastrus	Celtis	Cornus	Fraxinus	Hamamelis	Juglans	Liriodendron	Ostrya	Populus balsamifera	Populus deltoides	Prunus virginiana	Pseudera	Ptelea	Rhus	Salix longifolia	Smilacina	Smilax	Tilia	Ulmus	Vitis
Vessels more numerous.....	m	m		x	x	m	x	x	x	x	x	x	x	x	xw	m	m	x	x	m	xw	x
Vessels larger.....	x	m	m	mx	x	m	m	m	m	x	x	x	x	x	x	m	m	x	x	m	xw	x
Total area of vessels larger.....	x	m	m	x	x	x	m	x	x	x	m	x	x	m	x	x	xw	x	x	m	m	x
Walls of vessels heavier.....	x	m	m	x	x	x	m	x	x	m	m	x	x	x	x	x	xw	x	x	m	m	x
Walls of wood fibers heavier.....	x	m	m	x	x	x	x	m	x	x	m	x	x	x	x	x	xw	x	x	m	m	x
Lumen of fibers smaller.....	m	x	x	x	x	mx	x	x	x	x	x	x	x	x	x	x	m	x	x	m	m	xw
More growth rings in stem of given size.....	m		x	x	x	x	x	x	x	x	x	x	x	x	x	x	m	x	x	m	m	xw
More sclerenchyma and collenchyma.....	m	m	x	mx	x	m	x	mx	x	x	x	x	x	m	x	x	m	m	x	m	xw	x
Cork thicker.....	m	m	m	m	x	x	m	x	x	x	x	x	x	x	x	x	m	m	x	m	xw	x

A summary of stem characters is as follows:

Vessels more numerous	14	X-	7	M (1 same)
Vessels larger	9	X-11	M (2 same)	
Total area larger	17	X-	5	M
Walls of vessels heavier	16	X-	4	M (2 same)
Walls of fibers heavier	14	X-	6	M (1 same)
Lumen of fibers smaller	16	X-	2	M (2 same)
More growth rings	10	X-	6	M (3 same)
More sclerenchyma and collenchyma	15	X-	6	M (1 same)
Cork thicker	9	X-	8	M (1 same)

There is a tendency for the vessels to be larger in the mesophytic forms, but more numerous in the xerophytic, the area being greater in the xerophytic. A greater number of xerophytic forms have heavier walls of vessels and fibers and smaller lumen in the fibers, making a more woody cylinder. A majority of xerophytic forms have more growth rings to the given diameter than the mesophytic forms, showing slower growth under the more adverse conditions. A majority of xerophytic forms show an increase in mechanical tissue as well as in the wood and an increase in cork formation, though this is not so marked as one might expect. The internodes in the stem, in every case measured, were shorter in the xerophytic form.

The lianas seem more apt than the trees to show exceptions to the general stem situation. Their vessels are always extraordinarily large, but why they should often be larger and more numerous in mesophytic forms, when those of trees are not, is impossible to guess.

Discussion of theories

That the characters cited are due to the conditions under which the plants live, or have lived in the past, is undoubted, but what are the immediate causes remains to be proved by experiment. The purpose of this investigation has been to get at a few facts, but it may be of some interest to review a few of the theories:

Mrs. CLEMENTS (4) considered light the principal factor in the development of deep palisade. HABERLANDT (16) said that light does not influence the structure of this tissue but only its disposition, and that the reason palisade is developed is because

the products of assimilation ought to be carried away from the assimilatory cells by the shortest possible road, and the form of cells best fitted for this rapid transportation is the elongated form. WAGNER (29) reported that alpine plants exposed to decreased transpiration did not show a reduction in palisade, and concluded that not transpiration but assimilation was more effective in producing that tissue. PICK (25) thought the elongated form of the palisade is ancestral, but that for a strong development light is necessary; DUFOUR (9) agreed with him in this respect. STAHL (26) related palisade development to light. EBERDT (10) thought that increase in palisade development is caused by assimilation and transpiration working together, and that light in itself is never the cause that calls forth palisade parenchyma. VESQUE and VIET (27) concluded from their experiments that light and dry air (accelerating transpiration) result in a greater development of palisade. BONNIER (2) adds temperature to these two factors. KEARNEY (22) considers excessive transpiration accountable for both increased palisade and succulency. HEINRICHER (20) related equilateral structure to the vertical position of leaves and thought it due to sunny and dry situations, dryness being secondary to strong illumination, as some plants growing in damp situations have equilateral leaves.

As to conductive and mechanical elements, it has long been known that they are reduced in aquatic plants, in the water leaf of *Proserpinaca* being scarcely differentiated at all. If the supply of water is the limiting factor, one would expect an increase in these tissues the more xerophytic the conditions; but of course water is not the only factor, and with the plant out of water, its roots in the soil, its leaves in the air, the larger the plant, and consequently the farther apart the roots and leaves, the more complicated become the factors. GILG (14) found in the xerophytic family Restiaceae a mechanical ring of strongly thickened cells, which VOLKENS (28) explained as related to poor water supply. HABERLANDT (17) thought mechanical influences, if they do not pass beyond a certain limit, act on stereome as a stimulus for further building it up. KOHL (23) found that in some plants grown in damp air the sclerenchyma ring was entirely lost, xylem elements

less numerously developed, and bast bundles weak or gone, due, he said, to differences in activity of transpiration. JOST (21) found that in *Phaseolus* a great mass of vessels was formed, even if transpiration was reduced to the minimum, and says "transpiration can indeed influence the quality and quantity of the vessels, but is not the cause of their formation. If it were so, the stems of our trees would grow in thickness as long as they transpire, at least the whole summer through; which they do not do." HABERLANDT (18) relates the number and size of the ducts to the transpiring leaf surface. HARTIG (19) agrees with HABERLANDT and adds "in the damp air of a dense forest the inner spaces are much narrower than in an open stand." PFEFFER (24) considers that within certain limits the development of the conducting system is favored when an increased demand is made upon it. VOLKENS (28), in studies of desert plants, found a small development of water-conducting elements. CANNON (5) irrigated desert plants and compared their ducts with those of non-irrigated plants and found better development in the latter. The two results may not be inconsistent. VOLKENS' plants may have reduced leaf surface or developed succulency, thus reducing transpiration, and so in a way correspond with CANNON's irrigated plants.

Conclusions

Conditions in the dunes are severe for plant life, including direct illumination and reflection, extremes of temperature, strong winds, sand-blast, and sandy soil, the result of all these factors being increased evaporation. The presence of considerable water above the water-table makes conditions less severe than they otherwise would be. The response to these conditions by true dune plants is seen in the predominance of low vegetation, long roots, woody stems, thick leaves (which may be reduced, equilateral, evergreen, or folded), succulency, hairs, thickened epidermis and cuticle, deep palisade, sunken stomata, and well developed mechanical and conductive tissues in all parts.

Plants generally growing in mesophytic situations, when found also on the dunes, show the following modifications: *of the leaf*, increased thickness, decrease in depth and increase in surface-

extent of epidermal cells, increase in thickness of the outer wall of the epidermis and of the cuticle accompanied by ridging, increase in palisade, in hairs, in conductive and mechanical tissues; *of the stem*, decrease in the length of internodes, increase in the number of vessels and in the area of their cross-sections, giving greater conductive space, increase in thickness of the walls of vessels and of the fibers accompanied by decrease in lumen of fibers, giving more wood, increase in the number of growth rings in stem of a given size, showing slowness of growth, increase in mechanical tissues outside the wood, and increase in cork.

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